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GALLS IN HARSH ENVIRONMENTS

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Abstract.—Responses of various gallforming species to environmental stresses are evaluated on three scales of variation: geographical, within habitat, and within plant. Along elevational gradients, species diversity and densities decline at higher elevations. Within habitats, gall densities are lower on water stressed plants, in most cases. Within plant variation in branch age and vigor also elicits strong gallformer responses, although responses to this factor are more variable between species. Elevational gradients, local plant quality and within plant quality, considered collectively, are good predictors of how gall systems will be organized.

A variety of environmental stresses or harsh conditions operate on different scales to organize biological communities in nature. This paper considers three such scales of variation and their effects on gallforming herbivores: 1, elevational gradients, which give rise to heat and cold stresses at opposite ends of the gradient and may encompass hundreds of kilometers of host plant range in scale; 2, within habitat or locally stressful conditions, such as plant water stress and nutrient stress, which involve smaller populations of plants; and 3, within plant quality, where aging of individual branches modifies their value as resources, involving dynamics of individual plants. These three scales of stresses can affect the survivorship and fitness of herbivores directly, and also indirectly, by changing the quality of the resource—the host plant, with which the herbivore interacts in an intimate fashion.

There are several important reasons for understanding gallformer responses to these scales of variation: first, to see if gallformers exhibit a common response to environmental stresses. This would determine whether gallforming, as a form of herbivory, has a really unique and readily understood ecology, or if gallformers are as variable in their responses to environmental qualities as are other types of herbivores. One could reasonably predict common responses by gallformers across taxonomic lines because they all share several fundamental biological features, perhaps the most important being their dependence on vigorously growing, meristematic plant tissue to initiate gall development and ensure survival of their progeny.

These results may also be of more general value: By understanding how a species or group of species responds to variable conditions occurring biogeographically, within habitats and within plants, one could predict a great deal about how a biological community or portions of it will be organized at any point in space.

To address this I interviewed researchers working on a variety of gallforming

Table 1. Biogeographical patterns in gallforming herbivores.

Author, Plant	No. Gall Species	Elev. Range Considered	Species Response	Numerical Response
1. Sacchi,* *Salix* sp.	4	1690–2460 meters (M)	1 sp. drops out at 2460 M	no change
2. Hawkins et al. (1986), *Atriplex* spp.	8	low desert to 1690 M	3 spp. drop out in Mohave	many rare
3. Hartman (1985), *Tetradymia* sp.	>1	1122 to 1268 M	?	most rare
4. Fernandes,* many species	13	308 to 3877 M	only 1 spp. above 2770 M	?
5. Fay,* *Picea* sp.	1	2460 to 3570 M	—	rare above 3077 M
6. Waring,* *Larrea* sp.	11	277 to 1138 M	7 species drop out above 923 M	most rare

* = unpublished data.

systems to determine how the herbivore(s) of interest respond to environmental stresses.

Results and Discussion

Species diversity in the four multispecies gall systems considered declined as species dropped out with increasing elevation (Table 1) (no information on species responses was available from Hartman (1985), #3, and Fay, #5, is studying only one species). The result of this pattern is that community diversity will be lower at higher elevations.

Gallformer abundance, another component of community makeup, is also highly correlated with elevational change. In 4 of 5 systems for which density information was available, densities declined with increasing elevation (Table 1).

These results indicate that elevation, with the climatic features which accompany it, is a good predictor and determinant of species diversity and density in gallforming systems. Ultimately, two features of elevation may be operating to cause these patterns: gallforming may be especially adaptive at drier, lower elevations, where herbivores are exposed to strongly dessicating conditions, and nonadaptive at higher elevations due to prohibitively cold temperatures and reduced productivity in plants.

Decreasing species diversity at higher elevations and latitudes within the *Asphondylia* (Diptera: Cecidomyiidae) guilds on both *Atriplex* spp. and *Larrea tridentata* (DC.). Coville suggests that this pattern, when observed in gall studies where more than one host plant species is involved, is not merely a response to a decrease in host plant species across these gradients. The influence of climatic change on the radiation of these gallforming species deserves further consideration.

Within habitats, variability in plant water stress strongly affects gallformer distributional patterns (Table 2). In 4 of these 6 gallformer systems, fewer gallformers colonized water stressed plants, indicating that well watered, vigorously growing plants are preferred resources. In one case (Table 2, #1), survivorship was greater on well watered plants, indicating that well watered plants are also better resources for some gallformers.

Table 2. Gallformer responses to plant quality.

Author, Plant	Gallformer	Response to Stress		Nature of Response
		Water	Nutri.	
1. Price and Clancy (1986), *Salix* sp.	*Euura lasiolepis* Smith	–	–	reduced #'s and survivorship
2. Fay,* *Picea* sp.	*Adelges cooleyi* Parry	–	?	reduced #'s
3. Abrahamson,** *Solidago* sp.	*Eurosta solidaginis* (Fitch)	–	–	?
4. Hawkins et al., (1986) *Atriplex* spp.	*Asphondylia* spp.	–	?	reduced #'s
5. Waring,* *Larrea* sp.	*Asphondylia* spp.	+	?	increased #'s
6. Clancy,* *Salix* sp.	*Pontania pacifica* Marlatt	+	–	improved survivorship

* = unpublished data.
** = personal observation.

This pattern is not surprising because well watered plants grow more vigorously than do stressed plants, which may explain why they are better resources for many gallformers. The preference for water stressed plants in 2 cases (Table 2, #5 and 6) is enigmatic in light of this.

All gallformer species responded strongly to the condition of water stress in plants, regardless of the nature of the response itself. The number of species of *Asphondylia* was greater on stressed creosote bushes (Waring, unpublished data), so species diversity as well as densities are affected by plant water stress. The *Asphondylia* species colonizing *Atriplex* responded differently to water stressed plants by colonizing them less than well watered plants. Such a discrepancy within a gallforming genus suggests that the species of host plant involved is also an important determinant of herbivore response (Table 2). Likewise, within the willow system, the 2 colonizing sawflies (Table 2, #1 and 6) responded differently to water conditions within the same plant species (*Salix lasiolepis* Bentham), with *Euura lasiolepis* Smith (Hymenoptera: Tenthredinidae) colonizing stems on well watered plants and *Pontania pacifica* Marlatt (Hymenoptera: Tenthredinidae) colonizing leaves on water stressed plants. Both species survived more frequently on their respective plant types (Table 2). Clearly, the relationships of these herbivores and host plants are complicated, but the responses to plant water conditions are strong enough that an understanding of existing water conditions enables one to predict densities, species diversity and levels of survivorship in many gallforming systems within habitats.

A wide taxonomic range of gallformers responded strongly but variably to changes in within plant quality. In 4 of 6 cases gallformers were more abundant, and in one case, had increased survivorship on younger, vigorously growing branches (Table 3). In contrast, 2 other systems responded negatively to increased vigor with lower densities and survivorship (Table 3). In the *Asphondylia* guild on creosote bush, fewer species as well as individuals occurred on vigorously growing branches (Waring, unpublished data). So diversity and densities of gallformers vary considerably within plants due to this quality alone. In all systems,

Table 3. Gallformer responses to within-plant quality.

Author, Plant	Gallformer	Prefers Vigorous Growth	Response
1. Thoeny,* *Robinia* sp.	*Ecdytolopha insiticiana* Zeller	yes	increased #'s
2. Washburn and Cornell (1981), *Quercus* sp.	*Xanthoteras politum* (Bassett)	yes	increased #'s
3. Craig et al., (1986), *Salix* sp.	*Euura lasiolepis*	yes	increased #'s and survival
4. Frankie and Morgan (1984), *Quercus* sp.	*Disholcaspis cinerosa* Bassett	yes	increased #'s
5. Kearsely,* *Populus* sp.	*Pemphigus betae* Doane	no	decreased #'s and survival
6. Waring,* *Larrea* sp.	*Asphondylia* spp.	no	decreased #'s

* = unpublished data.

individual branches within plants increase or decrease in their susceptibility to galling as they age, with the direction of the response dependent on the system.

These galls became scarce at the upper ends of elevational gradients and locally on water stressed host plants, in most cases. All species responded strongly to within-plant changes, although the direction of the response varied. More studies must be undertaken to verify these patterns. In general, gallformers responded negatively to environmental and biotic stresses.

Elevational, within-habitat and within-plant stresses are straightforward and fundamental factors and are useful in understanding the dynamics of gall systems. In the case of *Asphondylia* spp. on creosote bush, for instance, the densities and numbers of these species will be greatest at lower elevations, on water stressed plants and in the older, less vigorous portions of plant canopies. Although these three levels or scales may operate differently, they will have the same effects on populations, such that more stress equals more galls and species. Consideration of each level adds more resolution to an understanding of how biological communities or portions of them will be organized.

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